NEW SPECIMENS OF PICROMOMYIDS (PLESIADAPIFORMES, PRIMATES) WITH DESCRIPTION OF A NEW SPECIES OF *ALVEOJUNCTUS*

MARY T. SILCOX[1]

KENNETH D. ROSE[2]
Research Associate, Section of Vertebrate Paleontology

STEPHEN L. WALSH[3]

ABSTRACT

Two new specimens attributable to the plesiadapiform family Picromomyidae are documented. One, a lower molar, represents a new species here named *Alveojunctus bowni*. This species is the largest and most derived picromomyid currently known, with an extremely simplified molar morphology. The second new specimen is a fragmentary lower jaw attributed to *Picromomys petersonorum*; the specimen includes the first complete lower central incisor known for a picromomyid. This tooth shows none of the derived features seen in microsyopid I_1s, providing no support for a tie to this family. Instead, it is most similar to I_1 in *Tinimomys graybulliensis*, supporting a close relationship between Picromomyidae and Micromomyidae.

KEY WORDS: Incisors, Picromomyidae, Micromomyidae, Plesiadapiformes, Primates, Teeth

INTRODUCTION

In 1996 Rose and Bown recognized a new family of plesiadapiform based on the discovery of associated right and left dentaries representing a new species, *Picromomys petersonorum*. This species is characterized by an enlarged P_4 with a wide, oddly flattened talonid and unusual, cusp-like, mesiobuccal expansions on the trigonids of M_{1-2}. *P. petersonorum* is also exceptional as one of the smallest primate-like animals ever described. The recent description of the "smallest primate" by Gebo et al. (2000) does not discuss *Picromomys*, presumably because the authors do not consider plesiadapiforms to be primates. A comprehensive phylogenetic analysis of dental, cranial, and postcranial features of a wide diversity of plesiadapiforms, euprimates, and other archontans indicates that plesiadapiforms are most appropriately considered primates (Silcox, 2001). The body mass estimates of *P. petersonorum* and the smallest Shanghuang primate discussed by Gebo et al. overlap, so it is unclear which species is actually the smallest described primate.

Rose and Bown (1996) also included a previously described species of plesiadapiform, *Alveojunctus minutus* Bown, 1982, in the Picromomyidae on the basis of similarities in the morphology of the enlarged P_4 and the shared presence of

[1] Department of Anthropology, Penn State University, 409 Carpenter Bldg., University Park, PA 16802.
[2] Department of Cell Biology and Anatomy, Johns Hopkins School of Medicine, 725 N. Wolfe St., Baltimore, MD 21205.
[3] Department of Paleontology, San Diego Natural History Museum, P.O. Box 121390, San Diego, CA 92112.
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low-crowned lower molars with shallow or absent hypoflexids, strongly mesially canted trigonids, twinned entoconid and hypoconulid separated by an entoconid notch, and weak or absent mesiobuccal cingulids. Hooker et al. (1999) challenged the link between *Picromomys* and *Alveojunctus*, suggesting that the relationships of the latter "will remain obscure until more material is found (p. 393)." These authors did not account for the close similarity in P_4 morphology seen in *Picromomys* and *Alveojunctus*, or for the molar characteristics shared by these two genera. Although further material of *Alveojunctus* may suggest a different resolution, the current evidence strongly supports the inclusion of both species in a taxonomic grouping to the exclusion of any other known plesiadapiform.

Rose and Bown (1996) presented a cladistic analysis to elucidate the wider relationships of the Picromomyidae. In spite of some general resemblances to Picrodontidae (e.g., low-crowned molars and strongly mesially canted molar trigonids), the results of the analysis suggested that these similarities are due to convergence and that picromomyids are most closely related to either uintasoricine microsyopids or micromomyids. Although the authors slightly favored the micromomyid tie, they conceded that formalizing this relationship taxonomically was premature given the paucity of the material available at that time. Subsequently, Stafford and Szalay (2000) opined that the Picromomyidae were a group of microsyopids, although this view was not supported by new specimens, a revised cladistic analysis, or a discussion of any character evidence.

This paper documents new specimens of the Picromomyidae, including the description of a new species of *Alveojunctus* based on a single lower molar from the Uintan of California. We recognize that naming a new species based on a single tooth is ordinarily an undesirable practice. In this instance, however, we deem it appropriate because of the extreme scarcity of this group, the diagnostic differences between the new specimen and known picromomyids, and the temporal and geographic separation between this specimen and the rest of the known material of the Picromomyidae. The other species of *Alveojunctus*, *A. minutus*, is known from only a few isolated teeth, and its holotype is also a lower molar, allowing the most appropriate comparisons to be made (Bown, 1982). To date, only nine specimens that can be confidently referred to the Picromomyidae (see below) have been discovered, seven of which are isolated teeth of *Alveojunctus*. This material is known from Wasatchian, Bridgerian, and Uintan deposits, indicating that the family existed for at least six million years. In light of the derived morphology exhibited by known picromomyids, compared to that of their likely closest relatives, the family probably originated significantly earlier. Previous to this report the geographic range of the Picromomyidae was limited to Wyoming— with the description here of a specimen from California the geographic range of this family is significantly increased. All of these indications show that the family is so rare that there can be no guarantee that any better specimens of the new species will ever be recovered.

Dental characteristics of known picromomyids are suggestive of a diet similar to that of the tiny extant marsupial feathertail glider, *Acrobates* (Rose and Bown, 1996), which feeds on a diet of insects, nectar, pollen, and possibly tree exudates (Fleay, 1947; Woodside, 1995; Nowak, 1999), although further study is required to rule out other possibilities (e.g., a diet of soft fruits).

A new specimen of *Picromomys petersonorum* that includes the first complete lower central incisor is also documented here. The morphology of this tooth provides new evidence on the wider relationships of the family.

Abbreviations used in text are as follows: FMNH, Field Museum of Natural History, Chicago, Illinois; SDSNH, San Diego Natural History Museum, San Diego, California; USGS, United States Geological Survey, Denver, Colorado; USNM, United States National Museum of Natural History, Smithsonian Institution, Washington D.C.

SYSTEMATIC PALEONTOLOGY

Order Primates Linnaeus, 1758
Suborder Plesiadapiformes Simons and Tattersall, *in* Simons, 1972
Family Picromomyidae Rose and Bown, 1996
Genus *Alveojunctus* Bown, 1982
Alveojunctus bowni, **new species**
(Fig. 1A)

Holotype.—SDSNH 31788, right M_1 or M_2. Only known specimen; collected by M. A. Roeder and S. L. Walsh in 1986.

Locality.—San Diego Society of Natural History locality 3373, early Uintan, upper tongue of the Friars Formation, Carmel Mountain Ranch housing development, Unit 15, San Diego Co., California.

Diagnosis.—$M_{1\ or\ 2}$ approximately 25-30% larger in linear dimensions than $M_{1\ or\ 2}$ in *Alveojunctus minutus*. Lower molar paracristid less well defined than in *A. minutus*. Strong, straight valley present between the protoconid and paraconid/metaconid, missing in *A. minutus*. Contrasts with *Picromomys petersonorum* (but not *A. minutus*) in the lack of cingulids on the lower molar, the buccal cristid obliqua resulting in the absence of a hypoflexid, the poor definition of the buccal cusps, and the absence of a protocristid and postvallid.

Etymology.—For Thomas M. Bown, in recognition of his valuable contributions to knowledge of Paleogene mammals generally, and particularly to the discovery and study of plesiadapiform primates including Picromomyidae.

Description.—The single known isolated tooth cannot be definitively identified as M_1 or M_2 (see Discussion). The lack of a distal expansion associated with an enlarged hypoconulid, present on M_3 of all plesiadapiforms except picrodontids, indicates that it is not likely to be M_3. It is very low crowned. The tooth has a straight mesial border, associated with a poorly demarcated paracristid and a paraconid that is situated far lingually on the tooth, being positioned just mesial to the metaconid. The paraconid and metaconid, although closely appressed, are separated by a notch, so that each cusp is distinct. A narrow talonid notch separates the metaconid and entoconid. These cusps are closely positioned, compressing the talonid notch, and effectively closing the talonid basin lingually (in spite of the absence of an entocristid). The lingual cusps are better defined than the buccal cusps, although all the cusps are low, broad, and bulbous swellings rather than sharp, pyramidal structures. The broadly swollen bases of the lingual cusps create a scalloped border to the central basin of the tooth (see below).

A chip of enamel is missing on the mesiobuccal margin of the protoconid, but the cusp appears to have been broadly based and displaced mesially, so that it is almost directly buccal to the paraconid. A faint postprotocristid extends down the distal face of the protoconid and merges with the cristid obliqua, which is fully buccal in position. The buccal border of the tooth is convex (although this is accentuated by the minor damage to the protoconid), so there is no sign of an indentation (hypoflexid) distinguishing the trigonid from the talonid. The presence or absence, or precise position, of a hypoconulid is unclear due to slight chipping of the enamel. The lingual cant to the back of the tooth is suggestive of a lingually positioned hypoconulid, but this cannot be confirmed. If a hypoconulid was present it must have been small, because the damage is very limited and there is no evidence of such a feature extending into the talonid basin.

There is no evidence of a protocristid or postvallid, making the trigonid and talonid basins continuous with one another. There is a straight, distinct valley between the protoconid and paraconid/metaconid that extends this composite basin even further mesially, to the front of the tooth. These
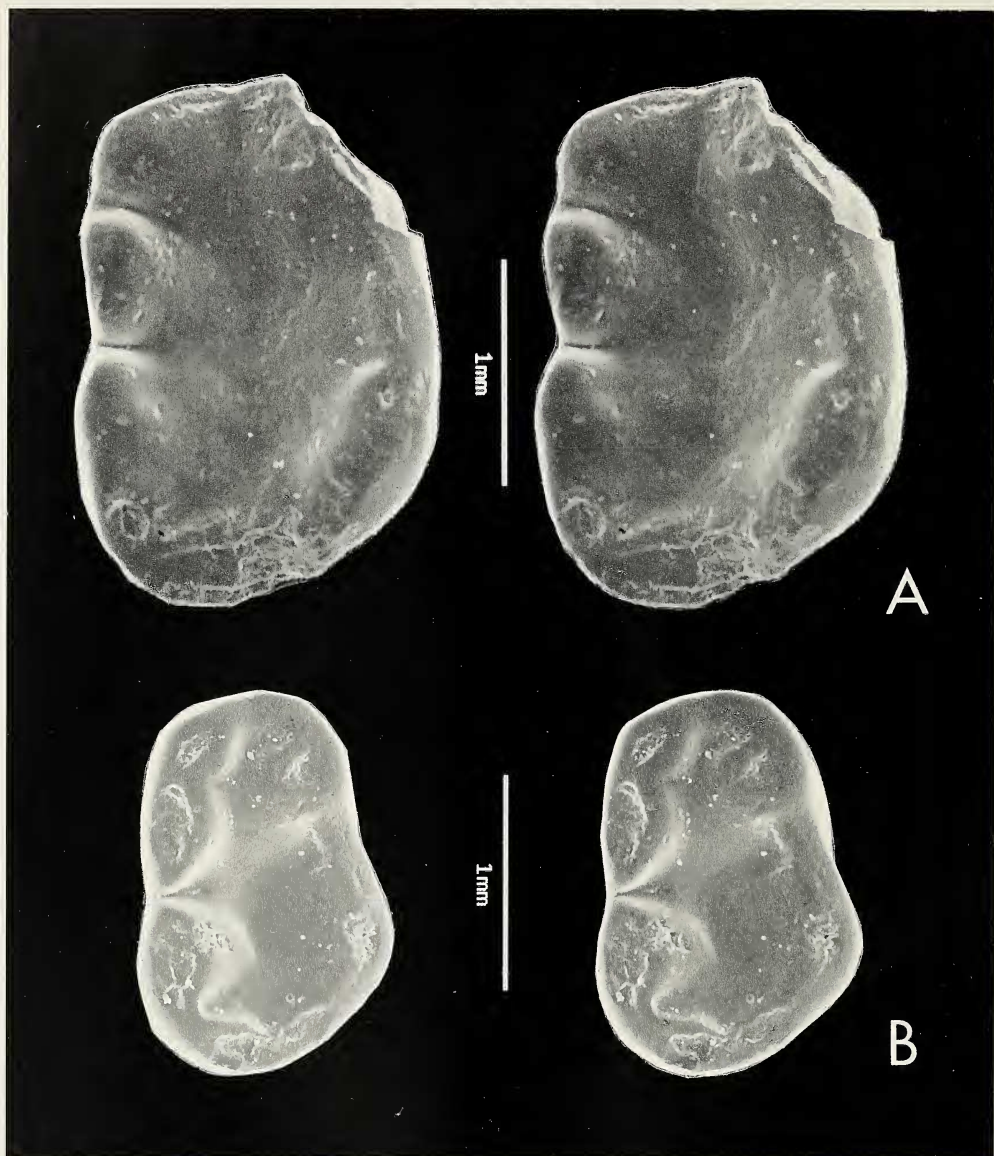
Fig. 1.—A. *Alveojunctus bowni*, new species, SDSNH 31788 (holotype), $RM_{1\ or\ 2}$, stereophotograph. B. *Alveojunctus minutus*, USGS 2005 (holotype), $RM_{1\ or\ 2}$, stereophotograph. Mesial is to the top of the figure and lingual to the left.

features make the crown of the tooth approximate a single, large, central basin surrounded on the periphery by low cusps and crests.

Measurements (mm) of the Holotype.—$M_{1\ or\ 2}$ maximum width = 1.60 mm, maximum length = 2.25 mm. Measured with an ocular micrometer to the nearest 0.05 mm.

Discussion.—SDSNH 31788 was tentatively assigned by Walsh (1996:85) to the ?Palaeanodonta. Its revised identification here as pertaining to a new species

of *Alveojunctus* thus eliminates any record of palaeanodonts from the Uintan of southern California.

SDSNH Loc. 3373 has yielded a diverse assemblage of small mammals of early Uintan age. It was collected by screen-washing approximately 5000 kg of bulk matrix from a 1.2 m thick, caliche nodule-bearing, olive greenish gray silt-stone paleosol. Other primate taxa represented at this locality include *Omomys* sp. cf. *O. carteri*, *Washakius woodringi*, and *Uintasorex montezumicus* (see Lil-legraven, 1980; Honey, 1990; Walsh, 1996). The stratigraphic and geographic position of SDSNH Loc. 3373 was shown schematically by Walsh et al. (1996: fig. 3).

The identification of SDSNH 31788 as M_1 or M_2 is complicated by uncertainty surrounding the identification of the holotype of *Alveojunctus minutus*, USGS 2005. This tooth was originally identified as an M_1 (Bown, 1982), presumably on the basis of the triangular trigonid that is relatively narrow compared to the tal-onid. M_2s in plesiadapiforms tend to have trigonid and talonid regions that are more nearly equal in width. Also, in M_2 the trigonid is generally less triangular than in M_1 as a result of its mesiodistal compression, a flatter mesial border, and a lingually positioned paraconid. These are also distinctions between USGS 2005 and the new specimen. In USGS 2005 there is a shallow hypoflexid, distinguishing the trigonid from the talonid (see Fig. 1B), that is missing in SDSNH 31788 (see Fig. 1A). Also, the flatter mesial border of SDSNH 31788 and more fully lingual position of the paraconid relative to USGS 2005 are consistent with differences between tooth positions (although there are some exceptions to these generalities, as seen in the lower molars of *Purgatorius janisae* and *Palenochtha minor*). Based on this reasoning it seems probable that USGS 2005 is an M_1 and SDSNH 31788 an M_2.

Rose and Bown (1996) suggested, however, that USGS 2005 is more likely M_2, based on its similarity to that tooth in *Picromomys petersonorum*. That taxon has a trigonid and talonid of M_1 that are subequal in width, whereas on M_2 the trigonid is clearly narrower than the talonid. *Picromomys* also has a relatively longer trigonid on M_1 than on M_2. In both of these features USGS 2005 is more similar to M_2 of *Picromomys* than to M_1. The straighter mesial border and more nearly equal width of the trigonid and talonid in SDSNH 31788 may make this more plausibly an M_1, based on the comparison with *Picromomys*. It is not clear, however, whether the unusual pattern of differences between M_1 and M_2 in *Pi-cromomys* stems solely from the different expression of the mesiobuccal accessory cusp in this taxon. Particularly, the greater development of this cusp on M_1, rel-ative to M_2, makes the mesial border of the tooth appear more squared off, and adds to the length and width of the trigonid. Since this cusp is missing in *Alveo-junctus* it might be expected to show the more typical plesiadapiform pattern of differences between M_1 and M_2. For these reasons, the attribution of the tooth is left open until further material becomes available.

This discussion may prompt the criticism that the differences between USGS 2005 and SDSNH 31788 can be attributed to tooth position alone. The pronounced size disparity between the specimens (we measured USGS 2005 as 1.80 mm long and 1.20 mm wide; SDSNH 31788 is therefore 25% longer and 33% wider than USGS 2005) argues against this. The size difference substantially exceeds that generally seen between tooth positions in plesiadapiforms—in *Picromomys pe-tersonorum*, for example, M_1 is only 10% longer than M_2, and M_2 is slightly wider (7%) than M_1. This dental size disparity also translates into a significant

difference in body size. If it is assumed that both molars are M_1, body mass estimates for *Alveojunctus minutus* range from 50–111 g (Conroy, 1987: all primate or prosimian regressions = 50 g; Gingerich et al., 1982: primate regression = 111 g), whereas the range of estimates for *Alveojunctus bowni* suggests it may have been twice the mass of *A. minutus* (Conroy, 1987: all primate regression = 124 g, prosimian regression = 114 g; Gingerich et al., 1982: primate regression = 238 g). These estimates do not differ significantly if one of the specimens is an M_2 rather than an M_1.

Additionally, the presence of the deep valley between the protoconid and paraconid/metaconid in SDSNH 31788 (missing in USGS 2005), argues against the view that both of these teeth belong to the same species. The presence or absence of a valley between the protoconid and paraconid/metaconid is not a difference that is seen between tooth positions, and this feature is missing in all related forms. The differences between USGS 2005 and SDSNH 31788 seem to be comprehensible as a further expansion, in the latter, of the broad central basin that is characteristic of *Alveojunctus*. In *A. minutus* this feature is formed because the protocristid and postvallid are absent, allowing continuity between the trigonid and talonid basins. In *A. bowni*, in addition to these features, there is a further expansion forward created by the strong valley between the protoconid and paraconid/metaconid. The reduction in the paracristid allows this valley to extend to the front of the tooth. The mesial displacement of the protoconid in *A. bowni* relative to *A. minutus* is probably also related, since this broadens the part of the trigonid basin that is directly continuous with the talonid basin. In all, the differences between the two species can be explained as an accentuation of the basic adaptive pattern that characterizes *Alveojunctus*, in which the molars became almost flat basins surrounded by weak bulbous cusps and low crests. The geologically younger age of *A. bowni* is also consistent with this view.

Alveojunctus bowni extends both the known temporal and geographic range of the Picromomyidae. To date, the genus *Alveojunctus* is definitively known only from middle Bridgerian and early Uintan deposits. Bown (1982) suggested that FMNH PM28689 might belong to *A. minutus*. This tooth, from the Cathedral Bluff Tongue (early Bridgerian), was attributed to *Niptomomys* sp. by West and Dawson (1973). West and Dawson identified the tooth as a right M_3, but the molar illustrated is a left M_3. Unfortunately, the specimen could not be located for study (and may be lost). The larger size of this tooth, relative to *A. minutus*, might suggest that the specimen could belong to *A. bowni*. FMNH PM28689 is unusual in lacking a paraconid, a feature that is present in both SDSNH 31788 and USGS 2005. The paraconid is absent on M_3 of paromomyid plesiadapiforms, and it is indistinct in *Niptomomys doreenae* (see Rose et al., 1993:fig. 1). In *Picromomys* and micromomyids known from serially associated dentitions (*Tinimomys graybulliensis* [Rose et al., 1993:fig. 2] and *Micromomys fremdi* [Fox, 1984:fig. 1]), however, a paraconid is clearly demarcated on M_3. Since we consider *Alveojunctus* to be more closely related to *Picromomys* and micromomyids than to *Niptomomys* or paromomyids, an indistinct M_3 paraconid would not be expected as a feature of the genus. These indications suggest that this tooth may be attributable to a taxon that is more closely related to *Niptomomys* (as originally indicated by West and Dawson) than to *Alveojunctus*.

Stucky (1982, 1984) referred an additional specimen to *Alveojunctus*. This isolated tooth, a right M_1, (UCM 44681) was not available for study. Stucky (1982) notes that this tooth has more clearly delineated cusps and a higher trigonid than

Alveojunctus minutus. In light of the fact that *Alveojunctus bowni* differs from *A. minutus* in precisely the opposite ways (i.e., it has a less well defined cusps and a lower trigonid), it seems unlikely that this specimen could be referred to the new species.

<center>

Picromomys petersonorum Rose and Bown, 1996
(Fig. 2)

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Discussion.—A fragmentary left dentary with a nearly complete I_1, P_4 talonid, M_1, and alveoli for M_{2-3} (USNM 494979; Fig. 2) was collected in 1996 by M. T. Silcox from Dorsey Quarry (U.S.G.S. locality D-2035Q; 397m above the base of the Willwood Formation; see Bown et al., 1994, and Silcox and Rose, 2001) in the Bighorn Basin of northwestern Wyoming. Although the I_1 has a break between the root and the rest of the tooth, and the crown is now displaced relative to the dentary, it was found in continuity with the dentary and is clearly part of the same specimen. The morphology of the P_4 talonid and M_1 matches that of the holotype of *Picromomys petersonorum.*

The root of I_1 is enlarged, laterally compressed, and is in a nearly horizontal position in the mandible, as in the holotype (Rose and Bown, 1996). It bears a distinct crest close to the lateral margin of the dorsal surface. Near the base of the crown this dorsal crest crosses from its lateral position to the medial side of the crown, where it descends onto the medial surface and runs distally to a point approximately halfway from the base of the tooth, before fading away. Near the point of this cross-over, another crest begins at the dorso-lateral extent of the crown. The two crests present on the crown of the tooth define a surface that exists in two planes, facing dorsally and medially.

Rose and Bown (1996) noted some basic differences between the morphology of the lower central incisor preserved in the holotype of *Picromomys petersonorum* and that seen in microsyopids. Although the holotype preserves only a part of the root of I_1, it is clear that I_1 lacks the sharp dorsal border and basal expansion characteristic of microsyopid incisors. Rose and Bown pointed out that the distinctive morphology of microsyopid incisors has resulted from a medial rotation around the long axis of the tooth, so that the homolog of the lateral border of I_1 in most plesiadapiforms forms a sharp dorsal crest in microsyopids. Rose and Bown (1996) argued that such a rotation had not occurred in I_1 of picromomyids. It remained possible, however, that when the rest of the crown became known it would be more microsyopid-like, or else represent a recognizable intermediate stage between the morphology observed in other plesiadapiforms and microsyopids.

The morphology of USNM 494979 does not support this view. The dorsal crest noted by Rose and Bown (1996) on the root is continuous with the medial crest on the crown of the I_1 in USNM 494979. In microsyopids, however, the dorsal crest is homologous with the lateral crest on the crowns of more typical plesiadapiforms (e.g., *Plesiolestes problematicus*; see Bown and Gingerich, 1973). This indicates that the I_1 morphology in *Picromomys* is not an intermediate on the path to the microsyopid condition. Furthermore, the shape of this incisor differs markedly from that observed in microsyopids in lacking a basal expansion of the crown. Also, the portion of the crown that is delimited by crests is not flat, as in microsyopids, but incorporates two distinct planes. In all, the picromomyid I_1 morphology is less consistent with a relationship to microsyopids than that ob-
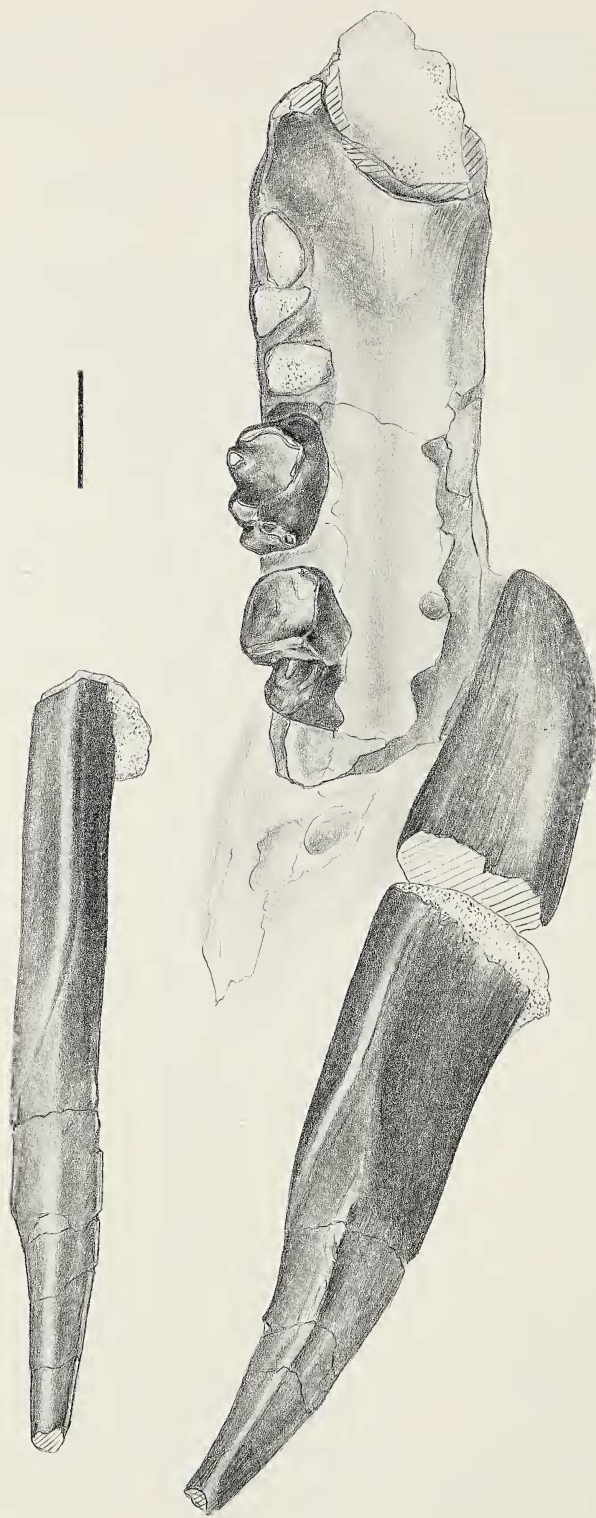
Fig. 2.—*Picromomys petersonorum*, USNM 494979. Incomplete left dentary containing I_1, talonid of P_4, M_1, and alveoli for M_{2-3} in oblique buccal view (below), with occlusal view of I_1 (above). Scale bar = 1 mm.

served in some palaechthonids. Even some primitive plesiadapoids have a more closely comparable incisor morphology (e.g., *Elphidotarsius* sp. cf. *florencae*, in which I_1 is broad at the base but not rotated medially; see Rose, 1975), in spite of the fact that plesiadapoids are not very closely related to microsyopids (Silcox, 2001).

The I_1 of *Picromomys* is similar to this tooth in a number of plesiadapiforms, including *Saxonella*, *Picrodus*, paromomyids, micromomyids, and possibly *Palenochtha minor* (see Gunnell, 1989:fig. 5), in being slender, laterally compressed, and elongate. The evidence available for *Purgatorius* is also consistent with the presence of this morphology, although the tooth itself is still unknown for this basal plesiadapiform (Silcox, 2001). The widespread distribution of this basic morphology suggests that it may be primitive for plesiadapiforms (Silcox, 2001). The lower incisor of *Picromomys* is particularly similar to that of the only micromomyid for which this tooth has been published, *Tinimomys graybulliensis* (i.e., USNM 425583, Beard and Houde, 1989). As in *Picromomys*, I_1 in *Tinimomys* shows a similar reorientation of a dorsolateral crest in the root region to a medial position on the crown. This change in direction in the dorsal crest is not present in any of the other plesiadapiforms examined. When added as a character to the dataset published by Rose and Bown (1996) (see Appendix), an exhaustive search using PAUP* 4.0β6 (Swofford, 2001) resulted in a single most parsimonious tree corresponding to their Tree B (length = 73 steps, CI = .49, RI = .537, statistics from PAUP*; see Rose and Bown, 1996:fig. 5). This tree supports a clade including *Picromomys*, *Alveojunctus*, and *Tinimomys*, to the exclusion of *Niptomomys*, and portrays picromomyids as most closely related to micromomyids.

Measurements (mm) of USNM 494979.—P_4 width = 0.80 mm; M_1 trigonid width = 0.70 mm, M_1 talonid width = 0.80 mm, M_1 length = 1.20 mm. Measured with an ocular micrometer to the nearest 0.05 mm.

Conclusions

This paper documents the eighth and ninth confidently attributed specimens of the Picromomyidae. The type specimen of the new species *Alveojunctus bowni* from the early Uintan of California extends the temporal and geographic range of the family. This specimen demonstrates an even more extreme version of the basic pattern of picromomyid dental structure, leading to an extraordinarily flat and simplified lower molar morphology. This is consistent with an increasingly specialized diet. The second recognized specimen of *Picromomys petersonorum* provides new information on the incisor morphology and suggests a stronger tie to the Micromomyidae than to the Microsyopidae. This may imply that Micromomyidae is a paraphyletic group (Hooker et al., 1999). Specifically, picromomyids and *Tinimomys* may be sister taxa to the exclusion of *Micromomys* (as indicated in Tree B of Rose and Bown, 1996:fig. 5). In light of this, it may eventually be appropriate to make Picromomyidae a subfamily of the Micromomyidae. Making definitive conclusions about the relationships of micromomyids and picromomyids is hampered, however, by the very limited information available for most species of *Micromomys* (Beard and Houde, 1989), and the lack of specimens from the upper dentition of Picromomyidae. Consequently, we prefer to maintain Picromomyidae and Micromomyidae as distinct families, pending further discoveries or additional analyses.

ACKNOWLEDGMENTS

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APPENDIX

New character added to cladistic analysis from Rose and Bown, 1996. 0 = lateral crest (or its homologue) in the root region of I_1 runs straight to the tip of the tooth, without crossing medially; 1 = A dorsolateral crest present in the root region of I_1 becomes re-oriented to lie on the medial side of the crown.

Purgatorius	?
Palaechthon	?
Palenochtha	?
Picromomys	1
Alveojunctus	?
Paromomys	?
Ignacius	0
Navajovius	0
Micromomys	?
Tinimomys	1
Niptomomys	0
Picrodus	0